THE PROGRESSIVE MOVEMENT OF GREGARINES.

BY HOWARD CRAWLEY.

I. Introduction.

While making observations on living specimens of *Stenophora juli*,[1] incident to a study of the life-history of this gregarine, I became impressed by the fact that Schewiakoff's currently accepted explanation for the progressive movement of gregarines does not satisfactorily account for all of the phenomena which the animals display. I was working at the time in the Zoological Laboratory of Harvard University, and at the suggestion of the Director, Prof. E. L. Mark, an investigation of gregarine movements of all sorts was undertaken. I desire to take this opportunity to express my sincere gratitude to Prof. Mark for the valuable aid which he rendered me.

The work was done almost exclusively on living animals, after the method used by Schewiakoff, which will be described below. *Stenophora juli*, from the intestine of *Julus*, and *Echinomera hispida*, from the intestine of *Lithobius*, were the species studied.

II. Historical and Critical.

The movements displayed by gregarines are of two kinds. The one, which consists of contractions of the body, is readily explainable by the existence of the muscular layer. The other, for which I shall use the term progression, is a movement of translation, during which the animal glides from place to place. It is usually described as taking place without the slightest bodily movement. This supposition, combined with the fact that gregarines possess no motor organs, rendered their progression apparently causeless, and until 1894, when Schewiakoff published his paper, it was regarded as one of the unsolved problems of biology. Prior to this date, biological literature contains but two suggested solutions of the problem. Lankester (1872, p. 347) says: " On slitting up a large

[1] The nomenclature used in this paper is that given by Labbé (1899).

Sipunculus, and allowing its abundant pink perivisceral fluid to run into a glass dish, my attention was attracted by two white flakes, of about an eighth of an inch in length, which were swimming actively in the liquid. Their movement was like that of some planarians, and seemed to depend on the undulation of their lateral margins, which were plainly to be seen in a state of vibration. These white flakes turned out to be specimens of *Monocystis sipunculi.*''

It is probable, however, that the movements here seen were nothing but the violent contortions which gregarines frequently show when first removed from their native environment. Such contortions might readily cause progression were the animals floating freely in a fluid. Moreover, Lankester himself appears never to have laid much stress on this single observation, for to my knowledge it is not referred to again in any of his later contributions on the Gregarinida.

Frenzel (1891 p. 287 *et seq.*) suggested that the progression of gregarines is due to a chemotactic affinity between them and their food. Such an explanation, however, is manifestly inadequate.

Schewiakoff (1894), as the result of a painstaking study, came to the conclusion that gregarines progress by means of the extrusion of gelatinous fibres. These fibres are derived from a layer of substance which is deposited between the cuticle and the ectoplasm. They pass out to the exterior through slit-like openings through the cuticle which occur in the grooves between the longitudinal thickenings. Upon their emergence, they do not project radially from the surface of the gregarine, but run backward until the posterior end of the animal is reached. Somewhat hardened by the action of the surrounding watery media, they then project backward and free of the animal. This extrusion, which takes place over the entire surface of the gregarine, results in the formation behind it of a hollow cylinder, the walls of which have by now acquired a certain amount of rigidity. The posterior end of this cylinder, impinging upon some resistant body, becomes fixed. The extrusion continuing, the cylinder lengthens, and the gregarine is pushed passively forward.

Schewiakoff undertook his studies in the light of Lauterborn's discovery that diatoms progress by means of the extrusion of gelatinous threads. There is a difference in the progressive movements of these two groups of organisms in that diatoms move indifferently in two directions, whereas gregarines always move forward. But in both cases the movement takes place without visible cause, and when Lauterborn showed that diatoms progress by means of the extrusion of threads of an invisible substance, a presumption was established that the cause for gregarine progression was to be sought for along similar lines.

Accordingly, Schewiakoff undertook a study of living gregarines. As mounting media, he employed either normal salt solution or an albumin solution of the following formula:

Egg-albumin, ...	20 cc.
Distilled water, ...	200 cc.
Sodium chloride, ...	1 gr.

Powdered carmine, Chinese black and, in some cases, native sepia were added to the fluid, so that invisible extrusions from the gregarines could be detected.

The results were to show that gregarines usually caught up and pulled after them a number of particles of carmine, etc., thus demonstrating the presence of a sticky substance. Further, as a gregarine progressed through a medium thickly filled with carmine particles, there was always left behind it a clear trail. Schewiakoff says that this does not happen with other Protozoa, and so furnishes proof that gregarines leave something behind them. This substance was wholly invisible under ordinary circumstances, but very delicate manipulation enabled him to stain it and to demonstrate that gregarines actually are followed by long fibres of extreme tenuity. Stress was laid upon the fact that carmine particles in the neighborhood of a motionless gregarine could be seen to show molecular movements; next to slip backward along the surface of the animal and to collect in a lump at the posterior end, and that only after this had taken place would the animal progress.

In the course of what follows, there will be frequent occasion to refer to Schewiakoff's statements, and the conclusions that he draws from them, in much greater detail. I have given above only his results, and a few of the more important observations upon which these results were based. His explanation of the cause of gregarine progression has been accepted by most authors, yet in some cases with a considerable amount of reserve. Lang (1901, p. 127) and Doflein (1901, p. 161) accept it without comment. Calkins

(1901, p. 149) says: "although very improbable at first sight, it is the only one thus far that fits the case." Wasielewski (1896, p. 22) rejects it, while Delage et Hérouard (1896, footnote on p. 261) say: "Pour bizarre qu'elle paraisse, il faut bien l'accepter jusqu'à nouvel ordre, car elle repose sur des faits observés et on n'en connait aucun autre à lui substituer."

Schaudinn (1900) and Siedlecki (1899) are credited with having confirmed Schewiakoff, the former by Lang (1901, p. 128) and the latter by Calkins (1901, p. 149).[2] Schaudinn (pp. 222–224) gives data which show that the sporozoïtes and merozoïtes of *Coccidium schubergii* extrude fibres of a gelatinous substance. These fibres carry backward such small particles as may be in the immediate vicinity of the coccidians, and form a trail behind them. In so far as the extrusion of a gelatinous substance is concerned, Schaudinn's observations unquestionably confirm those of Schewiakoff, but, as will be seen later, they do not necessarily show that this gelatinous substance is the cause of progression.

Siedlecki (1899, p. 521) says: "Es lässt sich aber bei *Monocystis ascidiæ* leicht noch ein anderer Bewegungsmodus beobachten: ohne irgendwie ihre Gestallt zu wechseln gleitet sie nämlich plötzlich vorwärts. Die Ursache der Bewegung liegt, wie es Schewiakoff für andere Gregarinen beschrieben hat, in einer plötzlichen Ausscheidung von Schleim aus dem Hinterende des Körpers, und es ist leicht festzustellen, wie das Thier durch einen aus ihm plötzlich herauswachsenden Schleimfaden vorwärts geschoben wird." This can scarcely be regarded as a confirmation of Schewiakoff.

III. Observations.

1. As a necessary preliminary, attention is here called to two points of considerable importance. The first of these concerns the shape of gregarines. The statement that gregarines are flat, like trematodes, is made in some text-books, but this is an error when applied to the Polycystidea. The gregarines of this group are monaxial animals, with a circular cross-section, and any plane passing through the axis divides them into morphologically identical halves. This is shown by sectioned gregarines, and it may readily be seen by watching the living animals.

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[2] The date, 1900, given by Calkins to Siedlecki's paper is incorrect.

The second point concerns progression. Gregarines are stated to show a "gliding" movement, and this, as we have seen, has been carefully studied. But I have been unable to find in the published literature on these animals any conclusive statement bearing upon the question as to whether gregarines creep or swim. Gliding could readily be effected in either of these two ways. When consideration is taken of their native environment, a very strong presumption is established that gregarines creep, yet certainly the matter is one which necessitates a demonstration.

This demonstration is not at all difficult. In all microscopic mounts, gregarines either lie against the under surface of the cover-glass or upon the slide, which can be shown by raising or lowering the tube of the microscope. Either the upper or under surface of the animals remains in focus until everything else has disappeared from view. This shows that all studies on progression have been made on animals which are in contact with a surface.

Gregarines possess and at times exert the power to progress continuously in straight lines. But more usually the progression is neither straight nor continuous. The animal advances by fits and starts, and the path pursued may be a zigzag or a series of curves. Plate I, fig. 1 shows the positions occupied by a progressing gregarine, *a* being the earliest and *f* the latest. To the right is sketched the line generated by any given point of the animal's body. Under such circumstances the advance is not continuous, but slow and hesitating, and accompanied by frequent stops. There may be an advance of perhaps the body length, followed by a short pause. Upon progression being resumed, it may be in the same or in a slightly different direction. The proper idea will be obtained by supposing the stops to take place anywhere along the broken line shown in the figure.

This mode of progression is very common, and at least in *Stenopohora juli* is much more frequently seen than continuous progression in a straight line. The alterations in the direction of the path are not, however, always so frequent as those shown in fig. 1, and the animal may advance along a series of curves. On the other hand, very short turns are often seen (Plate I, figs. 2, 3 and 4).

While progressing in any of these ways, gregarines may or may not display evident muscular movements. In all published accounts of gregarine progression, the statement is made that the animals glide forward without any alteration in the body form, and this is frequently the appearance. The converse statement, that gliding takes place while the animals are displaying evident muscular contractions, has never, to my knowledge, been made, although the fact itself can scarcely have escaped frequent observation. Yet progression without alteration in the outline of the body is no more frequently seen than progression accompanied by obvious muscular contractions. Gregarines may also progress, in either a straight line or in zigzags, with the body held rigidly in a contorted form. My observations here differ from those of Schewiakoff. On p. 348 he says that progressing gregarines may alter the direction of their progression, and continues: "In solchen Fällen bemerkt man jedes Mal, wenn die Bewegungsrichtung verändert wird, dass an der einen Seite der Gregarine eine Querfalte auftritt. . . . . Die Gregarine wird aus der früheren Bewegungsrichtung nach der Seite hin abgelenkt, auf welcher die Einschnürung am Gregarinenkörper erfolgte. Bleibt die Einschnürung längere Zeit hindurch bestehen, so wird die Bewegung bogenförmig, ja sie kann sogar zu einer spiraligen oder schleifenförmigen werden. Wird die Einschnürung aufgehoben, d. h., die Gregarine wieder gerade gestreckt, so wird die Bewegung von Neuem geradlinig." He believes that the bending of the body is the cause of the turning. For when the body is bent, the extrusion of the gelatinous fibres from the bent side is hindered. The result is a weakening of the propelling force on the bent side, with the natural result of a turning to that side. Straightening of the body brings about a uniform protrusion of the gelatinous fibres on all sides, with a resumption of progression in a straight line.

According to my observations, however, it is impossible to establish any definite correlation between alterations in the direction of progression and extensive muscular contractions. The animals may turn without the slightest bending of the body. As Schewiakoff says, they may turn and bend to the same side, but, on the contrary, they frequently turn to one side and bend to the other. Further, they may progress in a straight line with the body held rigidly in a contorted form, as stated above.

Progressing gregarines, without their progression being in any ways checked, will often bend and suddenly straighten with a jerk. This movement may take place a number of times and it has a certain bearing on the mode whereby progression is effected. The bending of the body necessarily throws either the anterior or the posterior end of the animal out of the line of progression (figs. 5 and 6). The former case (fig. 5) is not inconsistent with Schewiakoff's views, but the latter is (fig. 6). For such a movement would presumably detach the animal from the gelatinous stalk, yet it is effected with absolutely no pause in the progression.

Observations made on *Echinomera hispida* are equally suggestive. Fig. 7*a–d* shows the several positions successively occupied by a progressing individual of this species in making a turn. It will be seen that the animal bent sharply, so that the axis of the anterior part formed nearly a right angle with that of the posterior part. The narrow posterior part then swung rapidly around until it lay in line with the rest of the animal. It seems impossible to avoid the conclusion that this would have resulted in the breaking loose from any attached stalk, with the consequent cessation of progression. Yet there was not the slightest slackening in the speed of the animal, which was considerable.

2. On encountering obstructions, gregarines may simply slip off to one side or the other. Frequently, however, when an obstruction is met head-on, the protomerite holds its position for the moment and the animal swings to and fro like a pendulum. There may be one or two to several of these swings, after which the progressive movement may be resumed. This may take place without noticeable change in the shape of the body.

I am again obliged to differ with Schewiakoff, who (p. 343) says: "Trifft die Gregarine auf ein Hindernis, so steht sie einige Zeit still; es tritt dann eine Knickung am Körper der Gregarine auf, worauf die Bewegung in einer neuen, durch die Knickung des Vorderendes vorgezeichneten Richtung fortgesetzt wird." This may happen, but, according to my observations, more often there is no alteration in the shape of the body. It apparently depends upon the force with which the gregarine strikes the obstruction, this force being not necessarily powerful enough to cause the animal to bend.

I believe that the swinging to and fro tells strongly against the idea that gregarines are followed by an attached stalk of gelatinous fibres. It is not easy to see how such a swinging could fail to break the animal loose from any such stalk, whereupon it would come to rest. But this does not happen. Such a turn as that shown in fig. 3 may be a matter of only a second or two.

Another case is shown in fig. 4, where *a–f* show six positions successively occupied by a progressing gregarine. It is difficult to see how the gelatinous stalk can explain a progressive movement of this sort, which was seen a number of times.

3. Schewiakoff arrived at his conclusions partly from a study of the action of carmine particles, etc., in the vicinity of progressing gregarines. Such particles are seen to slip backward along the surface of the gregarine, and Schewiakoff believed they were being pushed or carried backward by the extruding gelatinous substance. He states that this takes place just before a gregarine begins to display a progressive movement, and continues during progression. This is true, but these particles show such varied movements that it is probable the extruding gelatin is not in all cases the cause. If the extrusion of gelatinous fibres be the cause of gregarine progression, then the rate at which the gelatinous fibres are passed backward should bear a direct ratio to the speed of the progressing gregarine. The movement of the particles along the animal's surface should mark the rate of extrusion, which should itself condition the rate of progression. But these particles may slip backward either more rapidly or more slowly than the gregarine is progressing. They may also slip rapidly backward along the surface of a gregarine which is not changing place, and further remain at a fixed point on the surface of a progressing individual. As a rule, the slipping is seen in progressing animals, but often it is not. Frequently a progressing individual causes little or no disturbance among the loose particles lying in its path, merely pushing them aside as it advances. The particles may also move forward along the animal's surface. This is seldom seen in progressing gregarines, but is frequent in those which are displaying changes of body form.

The movements of these small particles are so multifarious as to suggest that they are due to different causes. It is probable that surface tension is in part responsible. At the same time, the evidence that gregarines extrude a gelatinous substance is wholly conclusive. The animals are sticky, and will often remain adhering to the cover-glass in spite of rapid currents in the mounting fluid. I have also seen the substance arising from the surface of a progressing gregarine, and constituting a trail behind it. I made this observation but once, the gregarine being *Echinomera hispida.* With *Stenophora juli* I have never been able to see it. My observation differs from those of Schewiakoff in that the trail does not consist of fibres, but of a series of splashes (Plate II, fig. 8). The substance arose from the surface of the gregarine as short rods, which almost instanty expanded into irregular drops. These drops then became detached from the surface of the gregarine to constitute the trail.

I do not think that this observation gives any reason for questioning Schewiakoff's statement that the gelatinous substance passes backward as fibres. But since an extrusion of the sort shown in fig. 8 could hardly push the animal forward, the observation appears to me significant in indicating that the trail is the effect of progression and not its cause. It is an intrinsic weakness of Schewiakoff's explanation that it gives no reason why the gelatinous substance should pass backward instead of either forward or radially. If, however, the cause for progression is to be sought for elsewhere, it is easy to see why it passes backward. Upon its emergence on the surface of the gregarine, it is merely left behind, in precisely the same way as the mucus secreted by a snail is left behind as the animal advances. The passing backward of the gelatinous substance is the effect of progression, and not its cause.

As Schewiakoff states, progressing gregarines gather up and drag behind them masses of loose particles. The size of these masses is shown in figs. 9, 10 and 11. It often happens, however, that a gregarine may travel for a considerable distance without gathering up any such appendage. Except for perhaps half a dozen carmine particles or minute fat-drops, the animal drags nothing along behind it. This suggests that the quantity of adhesive substance on the surface of gregarines is subject to variation.

Whether Schewiakoff believes that the ability to extrude a gelatinous substance has been developed in gregarines for the purpose of locomotion does not appear. The extrusion of slimy substances by endo-parasites is, however, a common phenomenon, and we should look to find this power in a gregarine, just as we find it in a cestode.

In some cases, however, the sticky substance on the surface of gregarines appears to be derived from the host-tissue. To study gregarines, the method is to break up the appropriate host-organ on a slide, add a drop of some fluid, and place a cover-glass over the mount. There is necessarily released a quantity of various organic fluids, and these fluids are nearly always mucilaginous. That they are responsible for certain of the phenomena displayed by gregarines is suggested by the following observations, which also bear upon the question of gregarine progression. Fig. 12 shows a gregarine distant a trifle more than its own length from a solid mass of host-tissue. Between the gregarine and the host-tissue are a number of small particles. If an animal so situated be watched, it will be seen to advance slowly and unsteadily for a very short distance, possibly the half of its length, but usually much less. It will then stop, remain motionless for the fraction of a second, and finally, with a sudden jerk, return to the position which it occupied originally. The particles follow the movement of the gregarine, those nearest to it moving the greatest distance. This suggests that there is behind the gregarine a mass of an invisible, elastic substance, in which both the gregarine and the small particles are entangled. As the animal advances, this elastic substance is stretched, and when the force which has caused the animal to advance is released, it is brought back into its original position by the sudden shortening of the elastic substance.

This phenomenon, which was seen time and again, first caused me to question the truth of Schewiakoff's explanation of gregarine progression. For, if the advance be due to the elongation of a stalk behind the animal, this stalk should prevent the slipping backward. As will be developed later, I believe gregarine progression is due to slight muscular movements, not apparent under ordinary observational conditions. In such cases as the one now under consideration, the advance is resisted by the elastic sticky substance, and when the power is released the gregarine is jerked passively backward. Since it is those gregarines which are lying near the host-tissue which behave in this manner, it is probable that the elastic substance is derived in part from the host-cells. Gregarines some distance from any host-tissue were never seen to act in this way.

4. My studies had advanced to this point with no more result than to conclude that Schewiakoff's explanation of gregarine progression was probably incorrect. The case shown by fig. 12 suggested that the problem was to be solved by watching the gregarine

itself, although, assuming Schewiakoff to be incorrect, there was no other conclusion possible. The existence of locomotor organs, such as small cilia or temporary protoplasmic processes, was next considered. There was not, however, the slightest evidence for such organs to be detected with living gregarines, and the most rigid staining methods gave wholly negative results. Varying the observational conditions was next tried. I had been making my studies after the methods which I suppose have been generally employed in work on living gregarines. The highest powers used were those obtained with a one-eighth-inch dry lens and a No. 4 eye-piece. I had also followed the instinctive tendency to focus on the periphery of the gregarines, which results in studying no more than an optical section of the animals.

Knowing that *Stenophora juli* has the longitudinal elevations of the cuticle well developed, it occurred to me that they might furnish a means of getting at additional data. Accordingly, I began to make observations on the upper surface of the gregarines, using a one-twelfth-inch oil-immersion lens. It developed at once that this could not be done with ordinary illumination, on account of the opacity of most gregarines. But with the use of a lamp, it was easy to get an illumination sufficiently intense to render the gregarines almost transparent. The light was permitted to pass from the mirror to the sub-stage condenser without the interposition of blue or ground glass, and the diaphragm was left well open. The difficulty of managing a wet mount when studied under an oil-immersion lens was obviated in some cases by gluing the cover-glass to the slide with vaseline or spermaceti. This is not always necessary, for frequently the surface tension of the fluid of the mount will hold the cover-glass perfectly rigid.

This method very quickly revealed the fact that gregarines show a movement which hitherto appears to have escaped observation. This I shall designate as the *transverse movement*. It may be seen to take place when gregarines are behaving in any of the ways already described. It manifests itself as a shifting of the cuticular striations in a direction at right angles to the long axis of the animal. The more superficial granules of the endoplasm also take part in it, which indicates that the myocyte, or muscular layer, is involved. There is often to be seen in contracting gregarines a flow of granules which calls to mind the flow of granules seen in an amœba.

A deep constriction in the deutomerite will cause such a flow. The phenomenon just mentioned, however, is to all appearances of a totally different nature. It shows itself as a shifting, *en masse*, of all the granules in sight. There is no flowing, and, so far as it is possible to see, the granules maintain somewhat the same relative positions.

The reasons for supposing the muscular layer is involved in this phenomenon are as follows: The muscular layer lies upon and is directly continuous with the endoplasm. The latter is beset with granules to its extreme limit. Away from the surface, there is nothing to prevent a flow of these granules, but on the surface (of the endoplasm) it is not unreasonable to suppose that the netlike muscular layer entangles a number of these granules. In consequence, when the muscular layer contracts, the superficial granules are carried along with it. That there are granules embedded in the muscular layer is indicated by what is seen in plasmolyzed gregarines. In such animals, when the muscular layer is torn loose from the endoplasm, it always carries with it a number of granules.

The transverse movement is indifferently to one side or the other, or else to and fro. It is displayed conspicuously when the gregarine is behaving in the manner described on pp. 12 and 13, and illustrated in fig. 12. It also takes place when the animals turn, and frequently in such cases the cuticular markings and superficial granules are seen to sweep rapidly to one side, suggesting that the gregarine is rotating on its long axis. That such a rotation actually takes place can be confirmed by watching gregarines which have the nucleus out of the middle line, or some other mark which renders it possible to distinguish one side from the other.

In other cases there is nothing to demonstrate a rotation. The transverse movement is slight and slow, being first to one side and then to the other. This is seen when the animal is displaying the slow typical glide. Should the animal then turn, the transverse movement becomes more extensive and more rapid, while if progression be in any ways interfered with, a still greater increase in the speed and extent of the transverse movement takes place.

All of this occurs without the extensive muscular contractions which gregarines so frequently display. But it is possible to establish a correlation between the transverse movement and what is clearly a display of muscular activity. When a gregarine displays the common movement of a lateral displacement of the protomerite, or a bending just behind the septum, it can be seen with moderate powers that a wave of disturbance passes down the upper surface well to the rear end of the animal. Under high powers, with their limited focal depth, this wave is not readily seen unless it is the upper surface of the animal that is being watched. It is a very common phenomenon, and it establishes the fact that those muscular impulses which are most evident in the anterior part of the body make their influence felt nearly as far as the posterior extremity. Under moderate powers, it appears only as a wave passing down the upper surface, but if higher powers be used, it can be seen that this wave is the same as the transverse movement described above. That is, bending of the anterior part of the body causes a transverse movement of the cuticular striations and superficial granules. Moreover, the character of the bending bears a direct relation to the character of the transverse movement. When the bending is rapid and extensive, so also is the transverse movement, and it is under such circumstances that evident rotation may take place.

These phenomena are well seen in those animals which are entangled in some sticky elastic substance, as described on pp. 12 and 13, and shown in fig. 12. Such animals show frequently a more or less continuous bending of the anterior part of the body, and simultaneously the transverse movement.

In the case of animals which are gliding freely, the transverse movement is always much less extensive. With these it usually requires an oil-immersion lens to make satisfactory observations, with the result that it is altogether impossible, on account of the large size of *Stenophora*, to keep enough of the animal under observation at any one time to see if both the bending and the transverse movement take place together. Since, however, it is easy to see that an extensive bending is accompanied by an extensive transverse movement, it is supposable, by analogy, that the slight transverse movement is accompanied by slight bending.

I was able to obtain a certain amount of evidence that this is so. Observations were made on the protomerite of gliding gregarines, with the result of detecting frequent lateral displacements of this part of the animal. These movements were mostly so slight in extent that it required steady watching to detect them, and they would never be noticed with low or medium powers. They occur at frequent intervals. As stated above, *Stenophora* is so large that it is impossible to keep both the protomerite and the upper surface of the deutomerite in focus at the same time. But gregarines which showed these slight displacements of the protomerite were displaying the typical gliding movement, and such gregarines usually show the transverse movement. Moreover, by transferring the attention from the upper surface of the deutomerite to the protomerite, it was possible to see that both of these two sorts of movement take place at only very slightly separated periods of time.

It is evident that lateral movements of the protomerite which are at all evident must take place in a horizontal plane. A movement in a vertical plane would need to be far more extensive in order to be detected. Vertical displacements, however, can often be seen. That is, gliding gregarines move the protomerite indifferently in any direction. This appears to me a fact of considerable significance. It indicates that bendings of the protomerite may take place even when it is not possible to see them. Fig. 13 is a diagram of the anterior part of a gregarine. The solid line represents the longitudinal axis. The dotted line represents the axis of the protomerite when displaced in a horizontal plane. This displacement is so slight that it is clear, were it to be effected in a vertical plane, the highest powers and the most rigid attention would wholly fail to detect it.

It therefore seems reasonable to suppose that the transverse movement is directly correlated with either displacements of the protomerite or bendings of the body in the region of the septum. When both are extensive the connection is readily established, but when the transverse movement is slight, this can only be done by somewhat indirect means, as I have just pointed out. Yet it would be improbable that the transverse movement should at one time be correlated with bendings of the anterior part of the body, and not at other times, when the difference in the two cases is merely one of degree.

If, as I hope, my conclusions are warranted by the observational data, the cause for gregarine progression is extremely simple, and while the exact mechanics of the process are probably beyond observation, it may be suggested that it is effected in a manner somewhat as follows: The muscular impulse, starting backward from the region of the septum, necessarily causes the contact of the gregarine with the cover-glass to be different in this region from what it is in the more posterior parts. Further, since the transverse movement takes place at the same time as the backward movement, that part of the gregarine's surface where the contact relations are temporarily different moves not only backward, but from side to side as well. It is not difficult to see how movements of this sort may produce locomotion, when it be recollected that gregarines are sticky. If a particular part of the surface be in close contact with the cover-glass or slide, a muscular movement which carries this particular part backward would not be followed by a mere slipping of this part, but by a movement of the gregarine in the opposite direction. It is easy to see, when observing the upper surface of a progressing gregarine, that the contact relations of different parts are different. The upper surface loses its normal curved contour, and shows considerable irregularities. The observational conditions are too difficult to permit the changes of contour to be followed, and in consequence wholly direct evidence that progression is brought about in the manner outlined above is not to be had. It seems to me, however, that the explanation of gregarine progression here given is, on *à priori* grounds, more probable than that given by Schewiakoff, for it is based on the fact that gregarines possess a well-developed muscular system, and it is in line with the general principles of animal locomotion.

On the other hand, a passive locomotion by means of the extrusion of gelatinous threads is without parallel in the animal kingdom. Moreover, when the form of certain of the polycystid gregarines is taken into account, this mode of progression is almost inconceivable. Thus, *Porospora gigantea,* which inhabits the intestine of the lobster, is shaped like a serpent, and is about forty times as long as it is broad. Several genera, *Dactylophorus, Schneideria* and *Stichospora,* for examples, have the form of greatly elongated cones, with the posterior end terminating in a point. Specimens of *Echinomera hispida* frequently show an outline which recalls that of a tadpole. It is difficult to believe that the projection of gelatinous fibres from the extreme posterior ends of animals of this shape could push them forward.

It may not be amiss to call attention to the conditions in other Sporozoa. An adult coccidian possesses no muscular system, and lacks the power to move. On the other hand, intra-cellular gregarines, when squeezed out of the cells, show muscular contortions, and occasionally the typical progression of the free-living sporont. The Hæmosporidia and Myxosporidia, both of which are motile, possess muscle fibres similar to those of polycystid gregarines, whereas the Amœbosporidia (Schizo-gregarines) show no muscle, and are not known to possess the power to move. In general, throughout the Sporozoa, the possession of muscle fibres and the power of moving from place to place go hand in hand, while the forms which are not known to move lack muscular elements. It would, therefore, seem somewhat extraordinary if the polycystid gregarines, in which the muscular system is well organized, should have developed such a unique mode of progression as that described by Schewiakoff.

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EXPLANATION OF PLATES I AND II.

Plate I.—Fig. 1.—The successive positions occupied by a gregarine (*Stenophora juli*) progressing in a zigzag. The line to the right shows the nature of the path followed.

Fig. 2.—The successive positions taken by a progressing gregarine (*Stenophora juli*) when turning without alterations in the shape of the body.

Fig. 3.—The successive positions taken by a gregarine (*Stenophora juli*) after running head-on into an obstruction.

Fig. 4.—The same phenomenon as that shown in fig. 3. Here the change from *b* to *c* is accomplished in the same way as the change from *b* to *e* in fig. 3, and the change from *d* to *e* and from *e* to *f* in the same way as the change from the first to the last positions in fig. 2.

Fig. 5.—A progressing gregarine (*Stenophora juli*) throwing the anterior end out of the line of progression, which is shown by the ruled line. (This line is incorrectly drawn too far to the left.)

Fig. 6.—A progressing gregarine (*Stenophora juli*) throwing the posterior end out of the line of progression.

Fig. 7.—A progressing gregarine (*Echinomera hispida*) making a turn. Between *c* and *d* the narrow posterior end swung rapidly around until it lay in line with the rest of the animal.

Plate II.—Fig. 8.—The trail of gelatinous substance left behind by a progressing gregarine (*Echinomera hispida*).

Figs. 9, 10, 11.—The appendages of carmine, etc., which progressing gregarines gather up and drag behind them.

Fig. 12.—A gregarine (*Stenophora juli*) behind which are a number of small particles, lying near a mass of host-tissue. Both the gregarine and the small particles are entangled in an invisible, elastic substance (see pp. 12–13 of the text).

Fig. 13.—Anterior end of a gregarine (*Stenophora juli*). The solid line represents the longitudinal axis; the broken line the axis of the protomerite when displaced in the horizontal plane.